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Tropical secondary forest enrichment using giant stakes of keystone figs

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ABSTRACT

Developing rapid, cost-effective, methods to facilitate forest recovery in degraded tropical habitats is a key restoration goal. Here, we evaluated the efficacy of establishing large (≥ 2 m) vegetative cuttings or stakes of *Ficus* (Moraceae), keystone species that play essential roles in ecological food webs. We evaluated eight species with broad geographic distribution in the Neotropics in three separate studies in southern Costa Rica: (1) a common garden trial; (2) a multi-site study; and (3) an earlier 2004 study. In the two recent trials, resprouting and survival ranged from 0 to 100%. Six species of hemiepiphytic figs (subgenus *Urostigma*) resprouted at much higher rates (80–100%) compared to free-standing species in the subgenus *Pharmacosycea* (0–18%). Contrary to expectations, resprouting did not vary by wood specific gravity. Mean canopy area for established species was 1.1–1.4 m² after 2 yr, diameter growth at this stage was negligible, and one species developed fruit (~12% of individuals). In the older resurvey, surviving stakes (60%) had mean DBH of 13.7 ± 6.2 cm with canopy height of 8.1 ± 2.7 m after 13 yr; 50% of individuals were fruiting when surveyed during peak dry season. There was no mortality in the 9 yr lapse since they were last surveyed. Results indicate that this methodology shows promise and could be used to establish enrichment plantings in degraded habitats that augment fruit availability, and thereby facilitate recovery.

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Introduction

A core challenge in contemporary tropical conservation is to facilitate the colonization and establishment of late-successional species in young, regenerating forests. Secondary forests now compose more than half of tropical forests (Chazdon, 2014), and this ratio will continue to increase as old-growth forests are replaced by agriculture (Rudel, 2017) and marginal agricultural lands revert back to forest (Aide et al., 2013). Yet with few exceptions secondary forests do not support complete regional species assemblages (Gibson et al., 2011), and there is a considerable lag-time in recovery (Moreno-Mateos et al., 2017), with late-successional species particularly underrepresented (Martínez-Garza and Howe, 2003). Whereas tropical ecological restoration has often focused on establishing diverse forests on degraded sites (e.g., Lu et al., 2017;

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¹ Current address: Lyon Arboretum, University of Hawai'i at Mānoa, 3860 Mānoa Rd, Honolulu, HI 96822, USA. Rodrigues et al., 2009), developing mechanisms for secondary forest enrichment may be an important, cost-effective alternative to overcome dispersal and establishment limitations of sensitive species (Bertacchi et al., 2016).

Choosing appropriate species for secondary enrichment is an important consideration, and in the economy of nature, some species play larger roles than others. For example, keystone species are organisms that have a disproportionate ecological impact relative to their abundance or biomass, such that the removal of a keystone species from an otherwise intact ecosystem can precipitate major changes in ecosystem structure and function (Paine, 1974; Power et al., 1996). Reciprocally, establishing keystone species in degraded habitats may be an especially powerful means of catalyzing their recovery (Goosem and Tucker, 2013; Ripple and Beschta, 2007).

In tropical forests, figs (*Ficus* spp.; Moraceae) are a welldocumented example of a keystone group (Terborgh, 1986). Despite their relatively low abundance, fig trees support diverse animal communities through copious fruit production, and often do so at times of the year when few other food resources are available (Diaz-Martin et al., 2014; Harrison, 2005; Shanahan et al., 2001).

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R.A. Zahawi, J. Leighton Reid / Perspectives in Ecology and Conservation xxx (2017) xxx-xxx

By attracting a wide array of fruit-eating animals, fig trees also concentrate seed dispersal around them, creating hotspots of plant diversity (Fujita, 2014; Slocum, 2001; Slocum and Horvitz, 2000). With more than 800 species distributed throughout the world, several authors have concluded that figs should be included in efforts to restore degraded tropical and subtropical forests (Cottee-Jones et al., 2016; Dreschel et al., 2017; Kuaraksa and Elliott, 2013; Kuaraksa et al., 2012).

One promising technique for rapidly establishing figs on degraded lands is to propagate them as cuttings. Cuttings have several practical advantages compared to other revegetation practices like direct seeding and planting tree seedlings. Namely, cuttings do not require nursery care, they can be harvested at times when seeds are not available, they carry a lower economic cost than nurseryraised seedlings, and, by virtue of their greater height at planting, they may escape competition with ruderal vegetation more rapidly (Hunter, 1987; Zahawi and Holl, 2014). Moreover, cuttings are scalable; it is possible to plant large individuals that are several meters in length (Zahawi, 2008), and larger cuttings, including figs, tend to establish more consistently than do smaller cuttings (Danthu et al., 2002; Zahawi, 2005).

Successful establishment of large fig cuttings has been related to the time of year in which they are harvested (Alonso et al., 2000; Alonso et al., 2001). Several fig species are known to be easily propagated from cuttings, and planting fig cuttings is regularly practiced by rural people to produce live fence posts and to attract animals (Gautier, 1996; Harvey et al., 2005; Salick et al., 1995; Valerio, 2004). Animal attraction may be accomplished quickly, as fig cuttings taken from mature adults have been observed fruiting in the same year that they were planted (Zahawi, 2008; Zahawi and Holl, 2009). Whereas large cuttings are more cumbersome to transport, the effort may be worthwhile if a few planted individuals have a large effect on ecosystem recovery.

In this study, we address two questions about using fig cuttings for tropical forest restoration. First, what factors predict resprouting and establishment of native fig species in southern Costa Rica? Second, what is the long-term viability of fig trees planted as cuttings? To do so, we draw on three field experiments, two of which were established in 2015–2016 and a third long-term study that was initiated in 2004; we evaluate eight species of *Ficus*, each of which has broad geographic distribution in the Neotropics (Table 1).

Methods

Study area

Our study area comprises 13 sites spread across 53 km² of agricultural countryside in Coto Brus County, southern Costa Rica (Fig. 1). Site elevations range from 1000–1200 m a.s.l. The predominant native ecosystem is tropical premontane wet forest (Holdridge

et al., 1971), but most forest was cleared for coffee cultivation between the 1950s and 1980s with about 28% remaining in the study area at present (Zahawi et al., 2015). Today, the area is a diverse mix of coffee plantations, cattle pastures, crop agriculture, small urban centers, and forest fragments of varying ages. Precipitation varies with microtopography but is ~3600 mm y⁻¹ at the Las Cruces Biological Station (LCBS; 8°47' N, 82°57' W), with a distinct dry season from December to March. Mean annual temperature is $21^{\circ}C$ (LCBS, 2017).

Stake preparation

For the two planting trials in 2015–2016, we planted 4-m long cuttings (i.e., stakes) of eight native tree species in the genus Ficus. Following Zahawi (2008), stakes were harvested with a machete from multiple adults of each species, and all lateral branches were removed to limit dessication. Stakes were transported to sites in a pick-up truck and were cushioned to avoid damaging cortical tissue. Each stake was girdled 30 cm above the base immediately prior to planting in order to stimulate rooting just below the soil surface. Stakes were planted at 50 cm depth, and soil was lightly compacted around the base for stability. Mean stake diameter at breast height (DBH; 1.3 m) for all species at the time of planting was $(8.0 \pm 1.7 \text{ cm}; \text{mean} \pm \text{SD})$, and all stakes were planted within two weeks of cutting. For the long-term study we resurveyed stakes that were planted as 2-m tall cuttings in 2004 (Zahawi and Holl, 2009). Twenty individuals were planted at each of three field sites to a depth of 15–20 cm by opening a small hole using a stick and lightly compacting soil around the base of each planted stake. Given the shallower planting depth, stakes were not girdled.

Field trials

Common garden trial

To evaluate the resprouting capacity of a number of common, native *Ficus* species, we planted five stakes each of six species in a common garden within a young, secondary forest with a relatively sparse canopy (~5 m height) at the LCBS. Stakes were planted between 25 April and 15 May 2015, and species included *F. citrifolia* Mill., *F. colubrinae* Standl., *F. costaricana* (Liebm.) Miq., *F. hartwegii* (Miq.) Miq., *F. macbridei* Standl. (*N*=4 planted), and *F. obtusifolia* Kunth. Stakes were planted in a 5×6 grid with 3-m spacing. At planting time, we measured stake height and DBH. We monitored stake survival, establishment, and fruiting after 1, 2, 5, 8, and 22 mo. After 22 mo, we measured stake height, DBH, and canopy area, which we estimated as the area of an ellipse: πAB , where A and B are perpendicular radii.

Multi-site trial

To test stake performance across a heterogeneous landscape, we planted 145 individuals of four *Ficus* species in 11 young, secondary

Table 1

Resprouting, survival, and growth of six Ficus species planted as 4-m tall stakes in a common garden study and censused after 22 mo in southern Costa Rica.

Species	Geographic range ^c	No. planted	No. resprouted	No. surviving	Mean canopy area (m ²) (1 SD)
F. citrifolia ^a	US-Arg	5	5	1	1.4
F. colubrinae ^a	Mex-Col	5	5	3	1.5 (0.3)
F. costaricana ^{a,d}	Mex-Pan	5	5	4	1.6 (0.4)
F. hartwegii ^a	Mex-Per	5	5	5	1.4 (0.4)
F. macbridei ^b	Nic-Per	4	0	0	_
F. obtusifoliaª	Mex-Bra	5	4	1	1.0
Total		29	24	14	1.4 (0.3)

^a Subgenus Urostigma.

^b Subgenus Pharmacosycea.

^c Data compiled from Tropicos (www.tropicos.org).

^d Two of the four surviving individuals of *F. costaricana* that established were subsequently killed by falling tree limbs just prior to the final census.

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